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Horizontal distribution of calanoid copepods in the western Arctic Ocean during the summer of 2008

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Abstract

The horizontal distribution of the epipelagic zooplankton communities in the western Arctic Ocean was studied during August–October 2008. Zooplankton abundance and biomass were higher in the Chukchi Sea, and ranged from 3,000 to 274,000 ind. m⁻² and 5–678 g WM m⁻², respectively. Copepods were the most dominant taxa and comprised 37–94% of zooplankton abundance. For calanoid copepods, 30 species belonging to 20 genera were identified. Based on the copepod abundance, their communities were classified into three groups using a cluster analysis. The horizontal distribution of each group was well synchronized with depth zones, defined here as Shelf, Slope and Basin. Neritic Pacific copepods were the dominant species in the Shelf zone. Arctic copepods were substantially greater in the Slope zone than the other regions. Mesopelagic copepods were greater in the Basin zone than the other regions. Stage compositions of large-sized Arctic copepods (*Calanus glacialis* and *Metridia longa*) were characterized by the dominance of late copepodid stages in the Basin. Both the abundance and stage compositions of large copepods corresponded well with Chl. *a* concentrations in each region, with high Chl. *a* in the Shelf and Slope supporting reproduction of copepods resulting in high abundance dominated by early copepodid stages.

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1. Introduction

Recently a drastic reduction of sea ice cover area has been observed in the Arctic Ocean during summer. This reduction is thought to be primarily caused by an increased flow of warm Pacific Summer Water (PSW) from the Bering Sea Strait into the Arctic Ocean (Shimada et al., 2006; Woodgate et al., 2010). Since

PSW flows through the western Arctic Ocean, sea ice reduction in the Arctic Ocean is greater in this region: e.g., Chukchi Sea, East Siberian Sea, Canada Basin and Mendeleyev Ridge (Shimada et al., 2001, 2006; Stroeve et al., 2007; Comiso et al., 2008; Markus et al., 2009). These reductions of sea ice are expected to be cause for changes in the marine ecosystem structure in the Arctic Ocean (Hunt and Drinkwater, 2007). To evaluate the effects of sea ice reduction on marine ecosystems, studies on plankton community in the western Arctic Ocean are essential.

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Phytoplankton standing stock in the western Arctic Ocean has large seasonal and spatial variability (Springer and McRoy, 1993; Hill and Cota, 2005). Melting sea ice in the western Arctic Ocean during late spring to summer removes the sunlight limitation, which results in short-term phytoplankton blooms (peaks exceeding $8 \mu\text{g Chl. } a \text{ L}^{-1}$) (Springer and McRoy, 1993). After these blooms a subsurface maximum in the 20–40 m depth range appears, caused by inflow of dense, high nutrient Pacific Water under the low nutrient melting ice water (salinity < 30) (Cota et al., 1996; Hill and Cota, 2005).

Zooplankton is a secondary producer of marine ecosystems and is an important as food for pelagic fish and whales in the western Arctic Ocean (Lowry et al., 2004; Wassmann et al., 2006). In terms of zooplankton biomass, Arctic copepods, especially *Calanus glacialis* Jaschnov, *Calanus hyperboreus* Krøyer, *Metridia longa* (Lubbock) and *Pseudocalanus* spp. dominate the system (Longhurst et al., 1984; Conover and Huntley, 1991; Richter, 1994; Falk-Petersen et al., 1999; Kosobokova and Hirche, 2000; Auel and Hagen, 2002; Ashjian et al., 2003; Campbell et al., 2009). However, in the southern Chukchi Sea, large-sized Pacific copepods, (e.g., *Calanus marshallae* Frost, *Neocalanus cristatus* (Krøyer), *Neocalanus flemingeri* Miller, *Neocalanus plumchrus* (Marukawa), *Eucalanus bungii* Giesbrecht and *Metridia pacifica* Brodsky) dominate because of the Pacific Water inflow. Spatial changes in zooplankton biomass and community can then be attributed to the distribution of water masses (Springer et al., 1989; Lane et al., 2008; Hopcroft et al., 2010; Matsuno et al., 2011). Small-sized *Pseudocalanus* spp. are numerically abundant in the western Arctic Ocean, but because of the difficulty in species identification most of the existing studies have not identified copepods to species level (treated as spp.) (e.g., Springer et al., 1989; Lane et al., 2008). For the biomass dominant large-sized copepods (*C. glacialis*, *C. hyperboreus* and *M. longa*), identification down to copepodid stage level is not well reported (Lane et al., 2008).

In the present study, we evaluated the horizontal distribution of zooplankton abundance, biomass, community and population structures, and species diversity in the western Arctic Ocean during the summer of 2008. Analysis for small-sized copepods (*Pseudocalanus* spp.) and large-sized copepods (*C. glacialis*, *C. hyperboreus* and *M. longa*) were made down to the species and copepodid stages level, respectively. Based on these results, we discuss what parameters govern the horizontal distribution of copepods in the western Arctic Ocean.

2. Materials and methods

2.1. Field sampling

Zooplankton sampling was conducted at 54 stations located in the Chukchi Sea, Canada Basin and Mendeleev Ridge ($70^{\circ}00'–77^{\circ}41'N$, $174^{\circ}45'E–145^{\circ}00'W$) during 26 August to 8 October 2008 (Fig. 1). Zooplankton samples were collected during both day and night using vertical tows with a NORPAC net (mouth opening 45 cm, mesh size 0.335 mm) from 0 to 150 m (stations where the bottom was deeper than 150 m) or 5 m above the bottom (stations where the bottom was shallower than 150 m). The volume of water filtered through the net was estimated using a flow-meter mounted in the mouth of the net. Zooplankton samples were fixed with 5% buffered formalin immediately on board. Accompanying the zooplankton sampling, temperature and salinity were measured by CTD (Sea-Bird Electronics Inc., SBE 911 Plus) casts. Sea water samples were collected from ten discrete depths between 5 and either 200 m (stations where the bottom was deeper than 200 m) or between 5 m and 10 m above the bottom (stations where the bottom was shallower than 200 m) using Niskin bottles mounted on the CTD. Water samples were analyzed for nitrate, nitrite, ammonia, and phosphate using an autoanalyzer (Bran + Luebbe GmbH, TRAACS-800) on board. Chlorophyll *a* concentration was also measured using a fluorometer (Turner Designs, Inc., 10-AU-005).

2.2. Samples and data analysis

Post-cruise, zooplankton samples were split using a Motoda box splitter (Motoda, 1959). One aliquot was weighed for wet mass (WM) with a precision of 0.01 g using an electronic balance (Mettler PM4000). The remaining aliquots were used for identification and enumeration under a dissecting microscopic. Identification of calanoid copepods was made to the species and copepodid stage level. Species identification followed Brodsky (1967) and Frost (1989) for *Pseudocalanus* spp. (*Pseudocalanus acuspes*, *Pseudocalanus major*, *Pseudocalanus mimus*, *Pseudocalanus minutus* and *Pseudocalanus newmani*). For *Pseudocalanus* spp., species identification was made for late copepodid stages (C5F/M and C6F/M), and early copepodid stages (C1–C4) were treated as *Pseudocalanus* spp. For large-sized copepods (e.g., *C. glacialis*, *C. hyperboreus* and *M. longa*), the Mean Copepodid Stage (MCS) was calculated from the following equation:

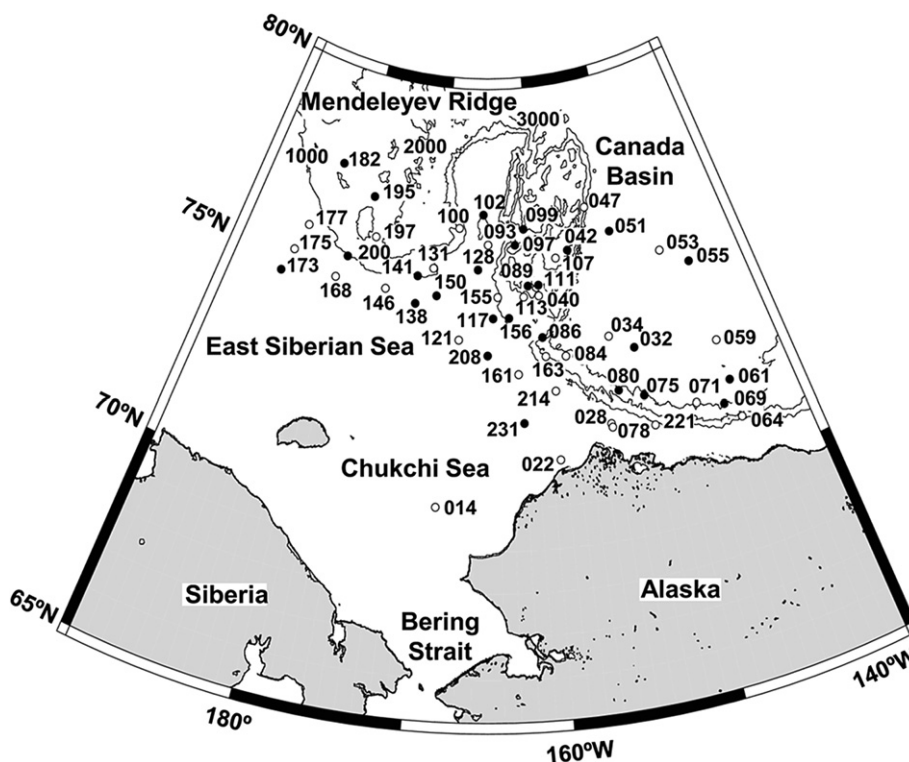


Fig. 1. Location of sampling stations in the western Arctic Ocean during August–October 2008. Open and solid symbols denote stations where sampling was conducted during day and night, respectively. Depth contours (1000, 2000 and 3000 m) are superimposed.

$$MCS = \frac{\sum_{i=1}^6 i \times Ai}{\sum_{i=1}^6 Ai}$$

where i (1–6 indicates C1–C6) is the copepodid stage, and Ai (ind. m^{-2}) is the abundance of the i th copepodid stage (cf. Marin, 1987).

To determine the wet mass of each copepodid stage, sufficient amounts of each copepodid stage (one individual for total length >3 mm or five individuals for ≤ 3 mm total length) were briefly rinsed with distilled water on nylon mesh, and water excluded from the samples. Specimens were transferred to the pre-weighed aluminum pan and weighed for wet mass (WM) with a precision of $1 \mu g$ using an electronic balance (Mettler Toledo MT5) (Table 1). Wet mass of each species was estimated by multiplying WM and the abundance of each copepodid stage.

The 54 sampling stations were evenly distributed for day ($n = 28$) and night ($n = 26$) sampling (Fig. 1). No significant differences were found between day–night data for most species and copepodid stages (total zooplankton abundance and biomass by U -test, $p = 0.13$ – 0.27 , *M. longa* abundance by U -test, $p = 0.43$). Therefore no day–night conversions of abundance and biomass data were made.

Abundance data (X : ind. m^{-2}) for each species was log transformed ($\log_{10}[X + 1]$) prior to analysis to reduce any bias in abundance. Similarities between samples were examined using the Bray–Curtis index (Bray and Curtis, 1957). For grouping the samples, similarity indices were coupled with hierarchical agglomerative clustering using a complete linkage method (Unweighted Pair Group Method using Arithmetic mean: UPGMA) (Field et al., 1982). Nonmetric Multi-Dimensional Scaling (NMDS) ordination was carried out to delineate the sample groups on a two-dimensional map. All of these analyses were carried out using BIOSTAT II software (Sigma Soft). Multiple-regression analysis was carried out between NMDS plots and hydrographic data (latitude, longitude, depth, integrated mean temperature and salinity of the net-towed water column). A species diversity index (H') in each group was calculated using the equation:

$$H' = - \sum n/Ni \times \ln n/Ni$$

where n is the abundance (ind. m^{-2}) of i th species and Ni is the abundance (ind. m^{-2}) of total calanoid copepods in the group (Shannon and Weaver, 1949). Inter-regional

Table 1

Mean wet mass (μg) of each copepodid stage of dominant calanoid copepods in the western Arctic Ocean during August–October 2008. n = number of measurements.

Species	Copepodid stage	Mean \pm sd	n
<i>Calanus glacialis</i>	C1	40 \pm 4	3
	C2	131 \pm 15	3
	C3	285 \pm 5	3
	C4	837 \pm 241	9
	C5	2,758 \pm 578	9
	C6F	3,946 \pm 732	9
<i>C. hyperboreus</i>	C6M	3,700 \pm 461	3
	C4	2,239 \pm 475	9
	C5	7,292 \pm 1,189	9
	C6F	17,984 \pm 1,939	9
<i>Metridia longa</i>	C1	26 \pm 2	3
	C2	54 \pm 8	3
	C3	143 \pm 48	3
	C4F	327 \pm 2	3
	C4M	276 \pm 7	3
	C5F	930 \pm 64	9
<i>Paraeuchaeta glacialis</i>	C5M	725 \pm 68	9
	C6F	2,341 \pm 162	9
	C6M	877 \pm 21	3
	C2	276 \pm 13	3
	C3	830 \pm 41	3
	C4F	2,771 \pm 95	3
<i>Pseudocalanus acuspes</i>	C4M	2,170 \pm 251	3
	C5F	8,137 \pm 1,041	9
	C5M	6,514 \pm 1,470	9
	C6F	23,704 \pm 3,729	9
	C6M	13,041	1
	C6F	146 \pm 9	3
<i>P. major</i>	C6F	231 \pm 8	3
<i>P. mimus</i>	C6F	127 \pm 39	3
<i>P. minutus</i>	C6F	224 \pm 19	3
<i>P. newmani</i>	C6F	82 \pm 21	3

differences in abundance of all copepods and *MCS* of large copepods were tested by one-way ANOVA and an ex post facto test by Fisher's Protected Least Significant Difference test (PLSD).

3. Results

3.1. Hydrography

Temperature and salinity in the upper 150 m ranged from -1.7 to 5.0 $^{\circ}\text{C}$ and 23.1 to 34.5 , respectively. The surface layer was characterized by high temperature and low salinity (Fig. 2). There were three distinct water masses in the study characterized by salinity and depth: Surface Mixed Layer Water (SMLW, salinity < 30 , depth 20 – 60 m), Pacific Summer Water (PSW, salinity 31 – 32 , depth < 80 m) and Pacific Winter Water (PWW, salinity < 33 , depth 80 – 150 m) (Shimada et al., 2001, 2006).

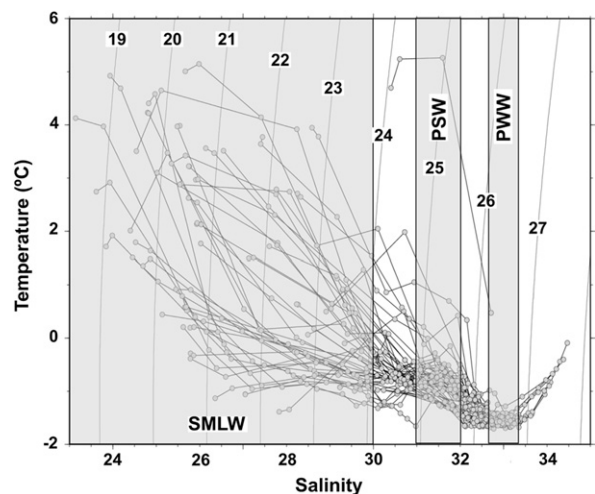


Fig. 2. T-S diagram between surface and 150 m (stations with bottom depth greater than 150 m) or 5 m above the bottom (stations with bottom depth shallower than 150 m) in the western Arctic Ocean during August–October 2008. Numbers in the panel indicate water densities ($\sigma\text{-T}$). Water masses are defined here as SMLW: Surface Mixed Layer Water (salinity < 30), PSW: Pacific Summer Water (salinity $= 31$ – 32 , depth $< \sim 80$ m) and PWW: Pacific Winter Water (salinity ≈ 33 , depth $= 80$ – 150 m) and are shown with shaded areas (cf. Shimada et al., 2001, 2006).

3.2. Zooplankton

Throughout the study area, zooplankton abundance and biomass ranged from $3,000$ to $274,000$ ind. m^{-2} and 5 – 678 g WM m^{-2} , respectively (Fig. 3). Both abundance and biomass were greater in the stations where the bottom depth was shallower than $1,000$ m. Copepods comprised 37 – 94% of zooplankton abundance and were the most dominant taxa (Fig. 4a). The most abundant copepods were small-sized *Pseudocalanus* spp. and large-sized *C. glacialis* and *M. longa*. Copepods comprised 3 – 82% of the total zooplankton biomass (Fig. 4b), with this biomass dominated by large-sized *C. glacialis*, *C. hyperboreus* and *M. longa* copepods. The percentage of small-sized *Pseudocalanus* spp. in the total biomass was lower than that of the abundance.

In the present study, 30 species of calanoid copepods belonging to 20 genera were identified (Table 2). Within these 30 species, 5 species: *C. marshallae*, *E. bungii*, *M. pacifica*, *N. cristatus* and *N. flemingeri* were Pacific copepods. Cluster analysis results based on the copepod abundance classified copepod communities into three groups at the 38% dissimilarity level (Fig. 5a). Each group was also easily identified in the NMDS plot (Fig. 5b). Several environmental parameters were significant in the NMDS ordination including

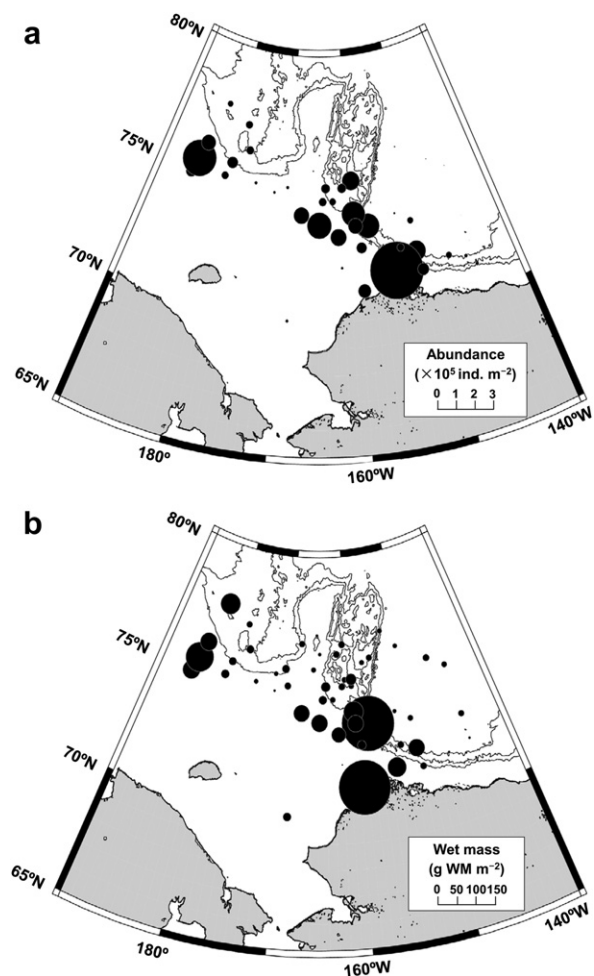


Fig. 3. Horizontal distribution of zooplankton abundance (a) and wet mass (b) in the western Arctic Ocean during August–October 2008. Note that the anomalously high biomass datum at St. 28 (678 g WM m⁻²) is omitted from (b).

depth, latitude, temperature and salinity ($r^2 = 0.35$ – 0.56), but note that longitude was not significant (Fig. 5b). The horizontal distribution for each group was well separated and varied with depth. As a result these groups were given regional terms, here listed from shallow to deep as: Shelf (4 stations), Slope (33 stations) and Basin (17 stations) (Fig. 5c). Species diversity (H') in the Shelf region was 1.79, but was substantially higher in the Slope and Basin regions (1.99–2.01).

Results of the inter-regional comparison on zooplankton abundance are shown in Table 2. The total abundance of zooplankton in the study area was greater in the Shelf and Slope regions, with the abundance in the Basin region being about 1/10 of the other two regions (Table 2). This was due to the higher abundance of

dominant *Pseudocalanus* spp. in the Shelf and Slope regions. The dominant species in the Shelf region were *C. marshallae*, *Centropages abdominalis* Sato, *Cyclopoida*, *E. bungii*, *M. pacifica*, *N. cristatus* and *P. minutus* (Table 2). Within these species, *E. bungii*, *M. pacifica* and *N. cristatus* originated in the North Pacific and migrate to the Arctic Ocean. In the Slope region, *C. glacialis*, *M. longa* and *Microcalanus pygmaeus* Sars were significantly more abundant than the other regions. Within these species, *C. glacialis* and *M. longa* were large-sized Arctic copepods. In the Basin region, *C. hyperboreus*, *Paraeuchaeta glacialis* Hansen and *Scaphocalanus magnus* T. Scott were significantly more abundant than in the other regions. These species were large-sized deep-water copepods with an adult body size larger than 5 mm.

For small-sized *Pseudocalanus* spp., the abundance and species composition of the C5 and C6 stages are shown in Fig. 6. The abundance of *Pseudocalanus* was greater in the Shelf and Slope regions than in the Basin region, and this pattern was common for the C5 and C6 stages (Fig. 6). The species composition showed regional differences (i.e. *P. acuspes* and *P. newmani* dominated in the Slope region, while *P. minutus* dominated in the Shelf and Basin regions), and this pattern was also common for both the C5 and C6 stages.

The copepodid stage compositions for large-sized copepods (*C. glacialis*, *C. hyperboreus* and *M. longa*) are shown in Fig. 7. *C. glacialis* in the Shelf and Slope regions was comprised of C1–C5 stages and characterized by the absence of the C6 stage (Fig. 7a). Composition of the C5 and C6 stages of *C. glacialis* was greatest in the Basin region. Throughout the study area, only the C4–C6 stages were observed for *C. hyperboreus* (no occurrence of C1–C3 stages for *C. hyperboreus*) (Fig. 7b). For *C. hyperboreus*, C4 was the dominant stage in the Slope, while C6 was the dominant stage in the Basin region. Stage composition of *M. longa* in the Shelf and Slope regions was primarily C1–C4, yet there was large variability between stations, as C5 and C6 were the dominant stages for several stations (Fig. 7c). Although the dominant stage of *M. longa* was C6 in the Basin region, C1–C4 stage organisms occurred in very limited extent. Regional comparison of MCS of each copepod showed that the MCS in the Basin region was significantly higher than in the other regions (Table 3). This indicated that the stage composition of large-sized copepods was dominated by late copepodid stage in the Basin region, which was observed for all three copepods (*C. glacialis*, *C. hyperboreus* and *M. longa*).

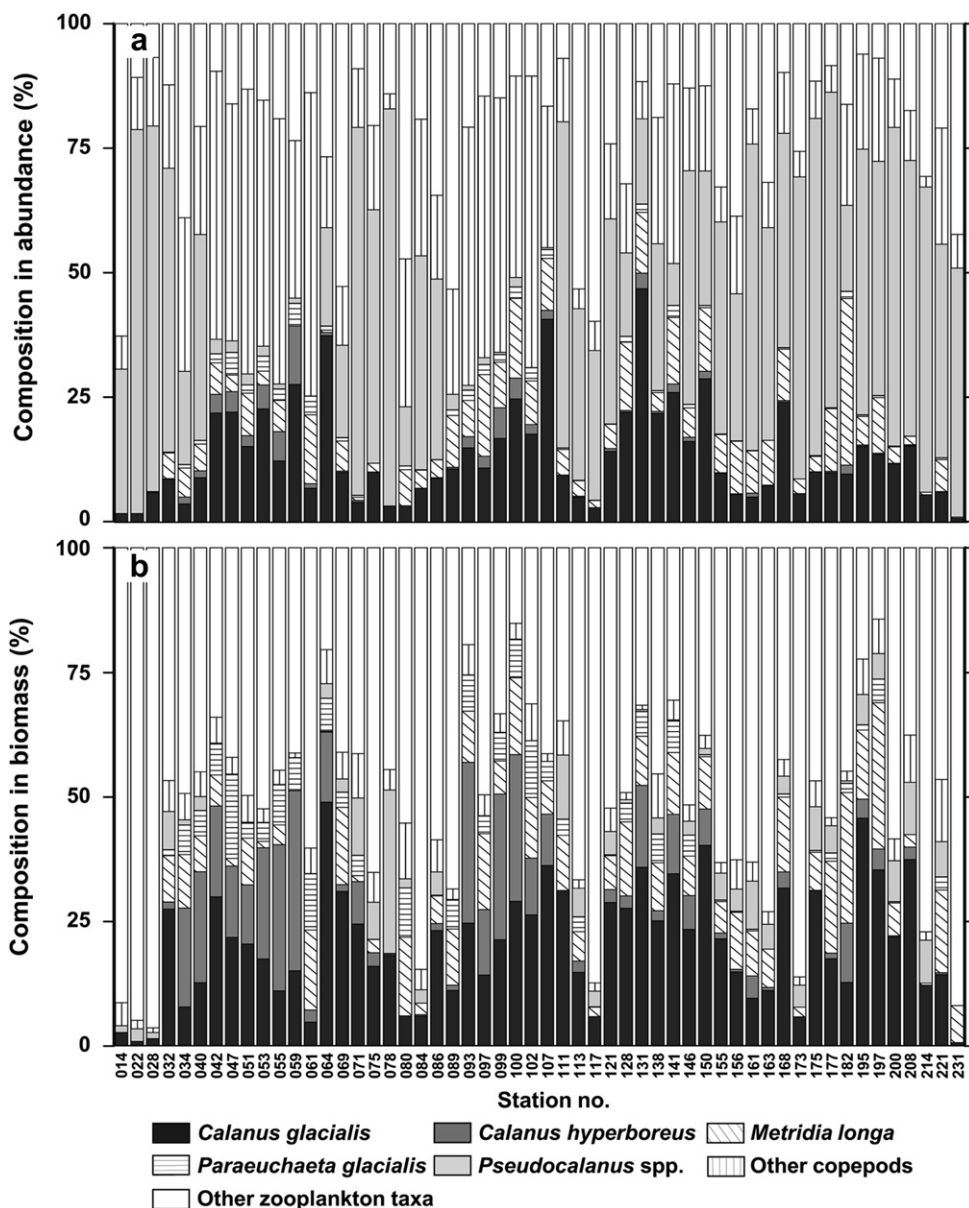


Fig. 4. Total zooplankton abundance (a) and biomass (b) in the western Arctic Ocean during August–October 2008. Shaded areas represent zooplankton groupings including dominant copepods.

4. Discussion

4.1. Zooplankton abundance, biomass and community structure

To compare reported values of zooplankton abundance and biomass in this study area (Lane et al., 2008), WM data was converted to dry mass (DM) assuming a water content of 81% (Omori, 1969). Obtained abundance (20–2,713 ind. m^{-3}) and biomass

(8–826 mg DM m^{-3}) in this study was lower (abundance) or higher (biomass) than previously reported values (abundance: 524–10,915 ind. m^{-3} , biomass: 3–58 mg DM m^{-3}) (Lane et al., 2008). These discrepancies may be caused by the differences in mesh size of plankton net used in each study. Lane et al. (2008) used 150 and 560 μm mesh size nets for abundance and biomass, while we used a 335 μm mesh size net for both abundance and biomass quantification. For abundance, the mesh size in this study was larger

Table 2

Comparison of copepod abundances in the three regions of the western Arctic Ocean during August–October 2008. The three regions were identified from a cluster analysis of copepod abundance using a Bray–Curtis similarity connected with UPGMA (cf. Fig. 5). Values represent the mean abundance in each region. Differences between regions were tested by one-way ANOVA and a post-hoc test using Fisher's PLSD. Any regions not connected by the underlines are significantly different ($p < 0.05$). Numbers in the parentheses indicate the number of stations included in each region. *: $p < 0.05$, **: $p < 0.01$, NS: not significant.

Species	Abundance (ind. m ⁻²)			One-way ANOVA	Fisher's PLSD		
	Shelf (4)	Slope (33)	Basin (17)				
<i>Acartia longiremis</i>	1,771	600	511	NS			
<i>Aetideopsis multiserrata</i>	0	59	0	NS			
<i>Aetideopsis rostrata</i>	0	12	0	NS			
<i>Calanus hyperboreus</i>	3	130	210	*	Shelf	Slope	Basin
<i>Calanus glacialis</i>	3,376	5,564	1,448	**	Basin	Shelf	Slope
<i>Calanus marshallae</i>	46	0	0	**	Basin	Slope	Shelf
<i>Centropages abdominalis</i>	995	80	0	**	Basin	Slope	Shelf
<i>Chiridius obtusifrons</i>	0	60	16	NS			
Cyclopoida	6,304	5,599	1,461	*	Basin	Slope	Shelf
<i>Eucalanus bungii</i>	60	2	1	**	Basin	Slope	Shelf
<i>Eurytemora herdmanni</i>	24	12	0	NS			
<i>Gaidius brevispinus</i>	0	17	0	NS			
<i>Gaidius tenuispinus</i>	0	5	0	NS			
<i>Heterorhabdus norvegicus</i>	0	17	25	NS			
<i>Metridia longa</i>	92	2,949	672	**	Shelf	Basin	Slope
<i>Metridia pacifica</i>	44	4	0	**	Basin	Slope	Shelf
<i>Microcalanus pygmaeus</i>	0	840	686	*	Shelf	Basin	Slope
<i>Neocalanus cristatus</i>	75	0	1	**	Slope	Basin	Shelf
<i>Neocalanus flemingeri</i>	12	42	1	NS			
<i>Paraeuchaeta glacialis</i>	0	112	150	**	Shelf	Slope	Basin
<i>Pseudocalanus</i> spp. (C1–C4)	28,614	14,710	179	**	Basin	Slope	Shelf
<i>Pseudocalanus acuspes</i>	10,017	8,337	47	NS			
<i>Pseudocalanus major</i>	1,711	1,410	9	NS			
<i>Pseudocalanus mimus</i>	357	537	1	NS			
<i>Pseudocalanus minutus</i>	4,702	374	29	**	Basin	Slope	Shelf
<i>Pseudocalanus newmani</i>	8,207	7,697	34	**	Basin	Slope	Shelf
<i>Racovitzanus antarcticus</i>	0	1	0	NS			
<i>Scaphocalanus magnus</i>	0	2	7	*	Shelf	Slope	Basin
<i>Scolecithricella minor</i>	0	51	50	NS			
<i>Spinocalanus longicornis</i>	0	11	13	NS			
<i>Tortanus discaudatus</i>	0	3	0	NS			
<i>Undinella oblonga</i>	0	3	0	NS			
Total copepods	66,407	49,254	5,550	**	Basin	Slope	Shelf
Total zooplankton	75,683	62,133	6,817	**	Basin	Slope	Shelf

than Lane et al. (335 vs 150 μm), and smaller-sized zooplankton (e.g., cyclopoid copepods) may have escaped collection in this study, providing an abundance estimate lower than those reported in Lane et al. (2008). For biomass however, a smaller mesh size was used than Lane et al. (2008) (335 vs 560 μm). This

may have allowed a better collection of smaller-sized zooplankton (e.g., *Pseudocalanus* spp.) in this study, resulting in a biomass estimate higher than those of Lane et al. (2008). While the quantitative values are different, the horizontal distribution patterns of zooplankton abundance and biomass (greater in the

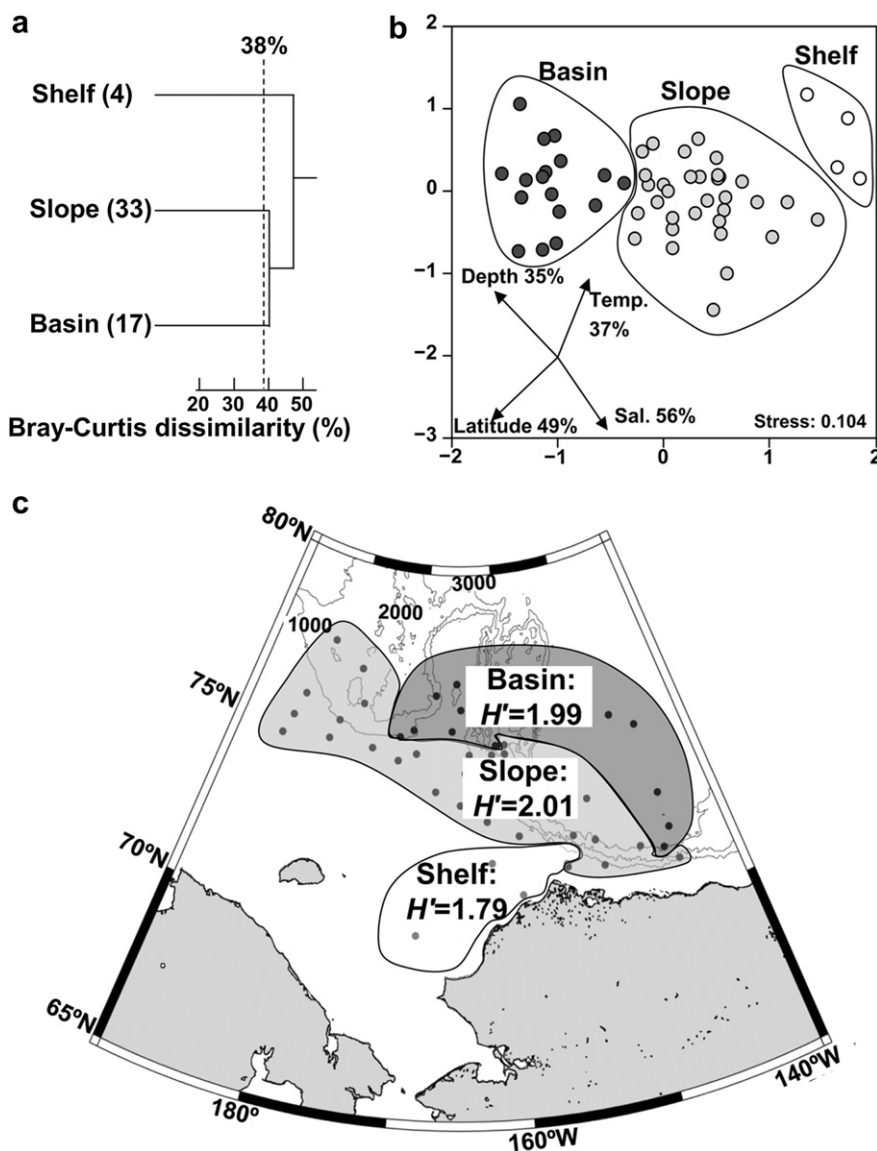


Fig. 5. Results of cluster analysis based on copepod abundance using a Bray–Curtis similarity connected with UPGMA. Three regions (Shelf, Slope and Basin) were identified using the 38% dissimilarity (dashed line) (a). Numbers in the parentheses in (a) indicate number of stations included in each region. Nonmetric multidimensional scaling plots of the three groups (b). Arrows and percentages in (b) indicate directions of environmental parameters and coefficient of determination (r^2), respectively. Horizontal distributions of the three groups in the western Arctic Ocean (c). H' indicate species diversity indices in each region.

Shelf and Slope regions) corresponded well with the results of Lane et al. (2008). We think that the application of the consistent mesh size (335 μm) used in this study has an advantage on the direct taxonomic evaluation of biomass-measured samples by collecting smaller-sized zooplankton.

Species diversity was higher in the Slope and Basin regions (Fig. 5). This high species diversity in these regions was caused by the occurrence of deep-sea copepods in addition to surface copepods. Since

species diversity of copepods in the Arctic Ocean is known to be greater in deep layers (Richter, 1994; Kosobokova and Hirche, 2000; Auel and Hagen, 2002), the occurrence of deep-sea copepods in Slope and Basin may induce high species diversity there.

4.2. Horizontal distribution of dominant copepods

The dominant species in copepod abundance and biomass were varied. For abundance, small-sized

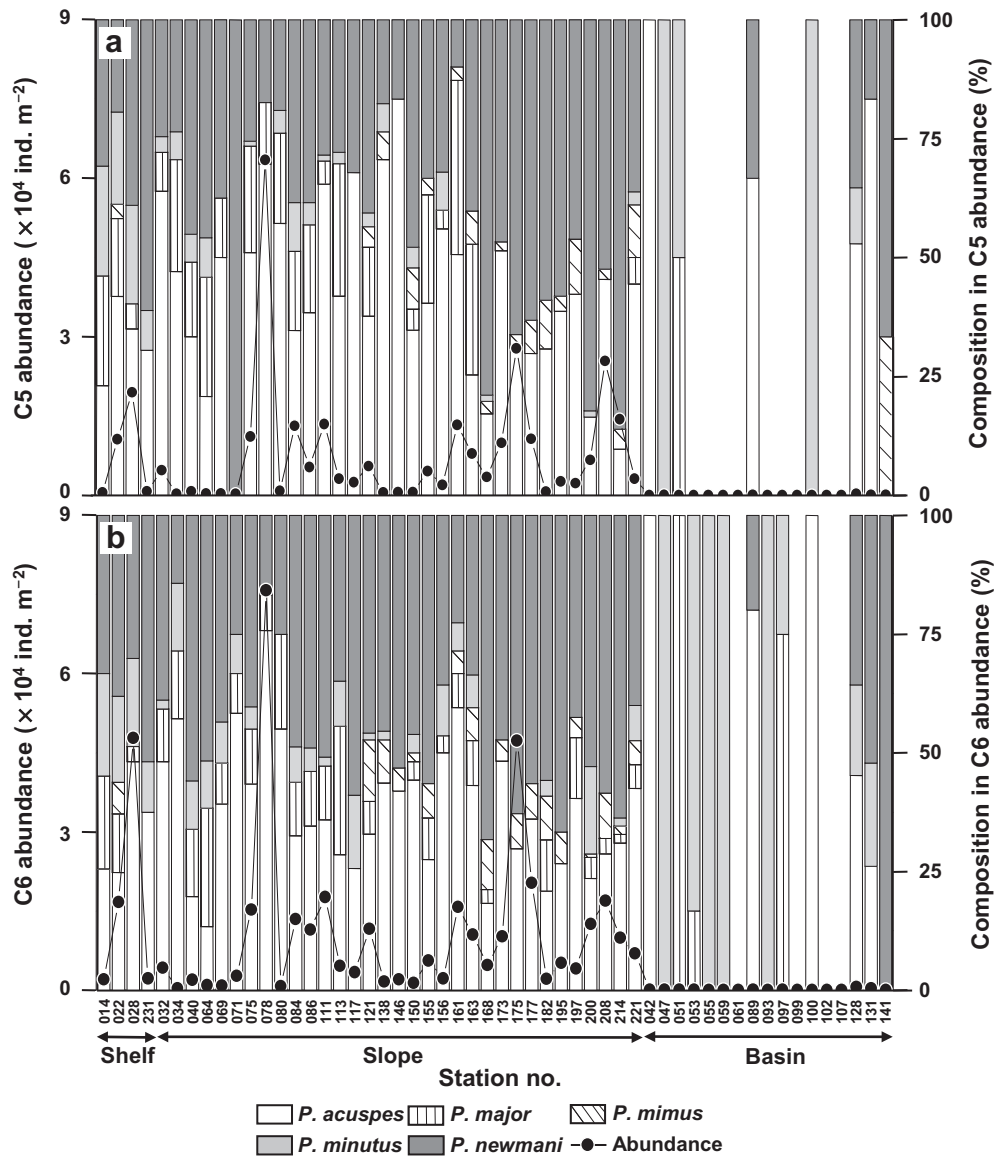


Fig. 6. Abundance and species composition of *Pseudocalanus* in stage C5 (a) and C6 (b) in the western Arctic Ocean during August–October 2008.

Pseudocalanus spp. was dominant, while large-sized *C. glacialis*, *C. hyperboreus* and *M. longa* dominated the biomass.

In the western Arctic Ocean, most previous zooplankton studies have not identified individuals in the genus *Pseudocalanus* down to species level (treated as spp.) due to the difficulty in species identification (e.g., Springer et al., 1989; Lane et al., 2008). In the present study, we made species identification on C5 and C6 stage *Pseudocalanus* and here show that five species: *P. acuspes*, *P. major*, *P. mimus*, *P. minutus* and *P. newmani* occurred in this area. The horizontal

distribution of each species was different, with *P. acuspes* and *P. newmani* dominant in the Slope region, and *P. minutus* dominant in the Shelf and Basin regions (Fig. 6). These species-specific horizontal distributions may be a reflection of their life cycle.

The life cycle of *Pseudocalanus* species has been studied at several locations in the Northern Hemisphere. *P. acuspes* reproduces during May–September, and rests with low metabolic activity in the C3–C5 stage during autumn to winter in the Baltic Sea and Norwegian fjords (Norrbin, 1994, 1996; Renz and Hirche, 2006; Renz et al., 2007). *P. newmani* in the

eastern coast of Canada and neighboring waters of Japan reproduces throughout the year and has no resting phase (McLaren et al., 1989; Yamaguchi and Shiga, 1997; Yamaguchi et al., 1998). *P. minutus*

stores lipids in prosome, descends down to 300–1000 m depths, and has diapause at the C5 stage during autumn to winter in the Arctic Ocean and Japan Sea (Richter, 1995; Yamaguchi et al., 1998).

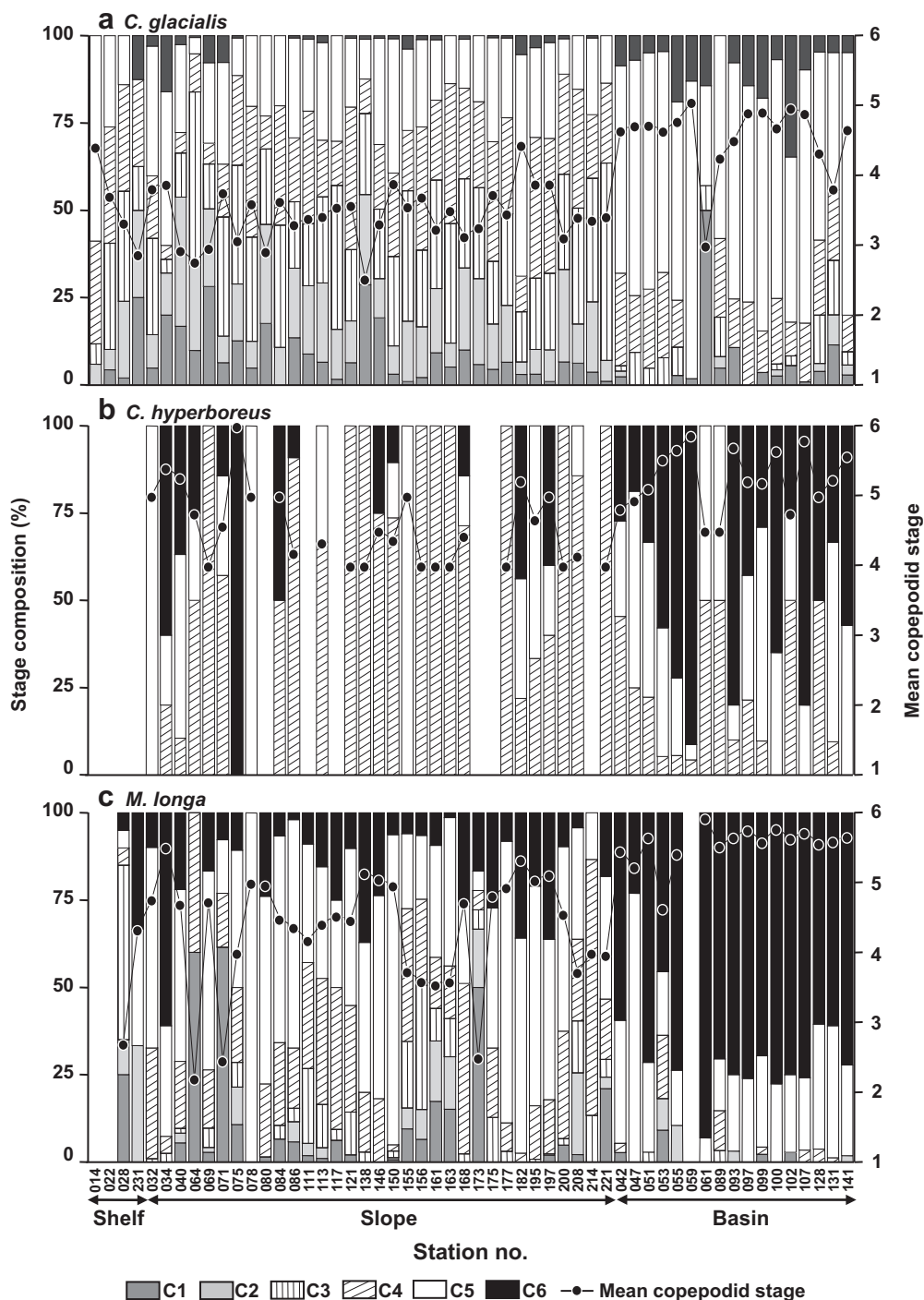


Fig. 7. Stage composition and mean copepodid stage of *C. glacialis* (a), *C. hyperboreus* (b) and *M. longa* (c) in the western Arctic Ocean during August–October 2008.

Table 3

Regional comparison in the mean copepodid stage of *C. glacialis*, *C. hyperboreus* and *M. longa* in the western Arctic Ocean during August–October 2008. The three regions were identified from a cluster analysis of copepod abundance using a Bray–Curtis similarity connected with UPGMA (cf. Fig. 5). Differences between regions were tested by one-way ANOVA and a post-hoc test of Fisher's PLSD. Any regions not connected by the underlines are significantly different ($p < 0.05$). Values are mean copepodid stage \pm sd. Numbers in the parentheses indicate the number of stations included in each region. **: $p < 0.01$.

Species	Mean copepodid stage			One-way ANOVA	Fisher's PLSD		
	Shelf (4)	Slope (33)	Basin (17)				
<i>C. glacialis</i>	3.58 \pm 0.65	3.44 \pm 0.07	4.56 \pm 0.12	**	<u>Slope</u>	<u>Shelf</u>	<u>Basin</u>
<i>C. hyperboreus</i>	No occurrence	4.55 \pm 0.55	5.24 \pm 0.44	**		<u>Slope</u>	<u>Basin</u>
<i>M. longa</i>	4.01 \pm 1.18	4.32 \pm 0.83	5.55 \pm 0.07	**	<u>Shelf</u>	<u>Slope</u>	<u>Basin</u>

The resting of *P. acuspes* is achieved by low metabolic activity at a slightly deep layer (Norrbín et al., 1990; Renz and Hirche, 2006), and not by deep descent as for *P. minutus*. In the present study, the dominance of *P. acuspes* and *P. newmani* in the Slope region might be a reflection of their extensive reproduction in an earlier season than the study period, while *P. minutus* was abundant in the Shelf and Basin regions. Since *P. minutus* has a diapause in the deep layer (Richter, 1995; Yamaguchi et al., 1998), they were abundant in the deep Basin region. The dominance of *P. minutus* in the Shelf region may be a result of upwelling of deep Pacific Water (which containing mass diapausing *P. minutus* in the C5 stage) exported through the Bering Strait into the Chukchi Sea. From these possible mechanisms, we propose that the horizontal distribution of *Pseudocalanus* spp. is related to their life cycle patterns.

The horizontal distribution of large copepods (*C. glacialis*, *C. hyperboreus* and *M. longa*) showed a species-specific pattern: i.e. *C. glacialis* and *M. longa* were greater in the Slope region, while *C. hyperboreus* dominated in the Basin region. While common to these three species, the copepodid stage composition was predominantly stages C5 and C6, and early copepodid stages were extremely rare in the Basin region (Fig. 7). All copepodid stages (C1–C6) occurred for *C. glacialis* and *M. longa* while only stages C4–C6 occurred for *C. hyperboreus*. These species-specific differences in horizontal distribution and stage composition may also be a reflection of their life cycle.

C. glacialis has a two-year life cycle in the Arctic Ocean (Conover and Huntley, 1991; Falk-Petersen et al., 1999). During the first summer they grow to the C3–C4 stage in the epipelagic zone, then migrate down to the deep layer to enter diapause. In second

summer they develop to the C5 stage in the epipelagic zone, then migrate down to the deep layer to molt to the adult stage (C6) using stored energy. During the third spring to summer they reproduce using the energy of the grazed phytoplankton bloom in the epipelagic zone (Longhurst et al., 1984; Ashjian et al., 2003; Falk-Petersen et al., 2009).

The generation length of the major population of *C. hyperboreus* in the Arctic Ocean has been reported to be three years, yet there is large reported regional variability (1–5 years) (Grainger, 1959; Dawson, 1978; Falk-Petersen et al., 1999). *C. hyperboreus* reproduce using stored lipids as energy in the deep layer (200–500 m) during October–March. Released eggs hatch and develop while floating up to the surface layer (Hirche and Niehoff, 1996). During the first summer they feed on phytoplankton and develop to stage C3, then store lipids and migrate down to 800–1500 m. During the second summer they ascend to surface, develop to stage C4, and enter diapause in the deep layer again. During the third summer they ascend to the surface, develop to stage C5, then descend to 200–500 m and molt to adult (Vinogradov, 1997). The dominance of the C6 stage in the deep basin in this study (Fig. 7b) corresponds well with the previous report (Vinogradov, 1997). The duration of development at the surface also varies greatly by region. This regional variability results in regional differences of generation length (1–5 years) for *C. hyperboreus* in the Arctic Ocean (Falk-Petersen et al., 2009).

While the two *Calanus* species in this study have a resting phase (diapause), the life cycle of *M. longa* is characterized by having no resting phase (Båmstedt and Ervik, 1984; Grønvik and Hopkins, 1984). These differences in life cycle may be related to their feeding modes. *M. longa* is considered to be omnivorous while

the two *Calanus* spp. are considered to be herbivorous (Haq, 1967; Barthel, 1988). In the food-limited winter, *M. longa* is reported to graze on floating eggs and the nauplii of *C. hyperboreus* (e.g., Haq, 1967; Sell et al., 2001).

From the viewpoint of their life cycle, *C. glacialis* and *M. longa* reproduce at the surface by grazing on phytoplankton or microzooplankton. The results of this study showing the dominance of early copepodid stages in Shelf and Slope may be the reflection of high prior reproduction in the Shelf and Slope during spring to summer. As reproduction of *C. hyperboreus* occurs in the deep layer (Falk-Petersen et al., 2009), their abundance was correspondingly high in the Basin region and extremely low in the Shelf region (Table 2). Since samples were only collected in the upper 150 m, early copepodid stages of *C. hyperboreus* may not have been collected, which may be why only stages C4–C6 occurred in this study (Fig. 7b).

4.3. Factors controlling copepod community

Since copepod reproduction energy comes from surface phytoplankton or microzooplankton, the

composition of early copepodid stages of *C. glacialis* and *M. longa* is considered to be a reflection of the amount of phytoplankton-microzooplankton in the region. All three large copepods had extremely low abundances of early copepodid stages in the Basin region (Fig. 7). This would suggest that the amount of phytoplankton was very low in the Basin region. Additionally, the abundance of small-sized *Pseudocalanus* spp. was lower in the Basin region than the other regions. Since the body size is smaller, and generation length is shorter for *Pseudocalanus* spp., their abundance is thought to quickly respond to the amount of available phytoplankton. Thus, both the abundance of small-sized copepods and the stage composition of large-sized copepods suggests that there are horizontal differences in phytoplankton stock (e.g., low in the Basin region). To explore this further, we can explore the regional differences in nutrients and phytoplankton stock (Chl. *a*), and evaluate the factors controlling abundance and stage composition of copepods.

Vertical profiles of temperature, salinity, dissolved inorganic nitrogen (DIN) and chlorophyll *a* (Chl. *a*) in the three regions are summarized in Fig. 8. Clear regional differences were detected for salinity, DIN

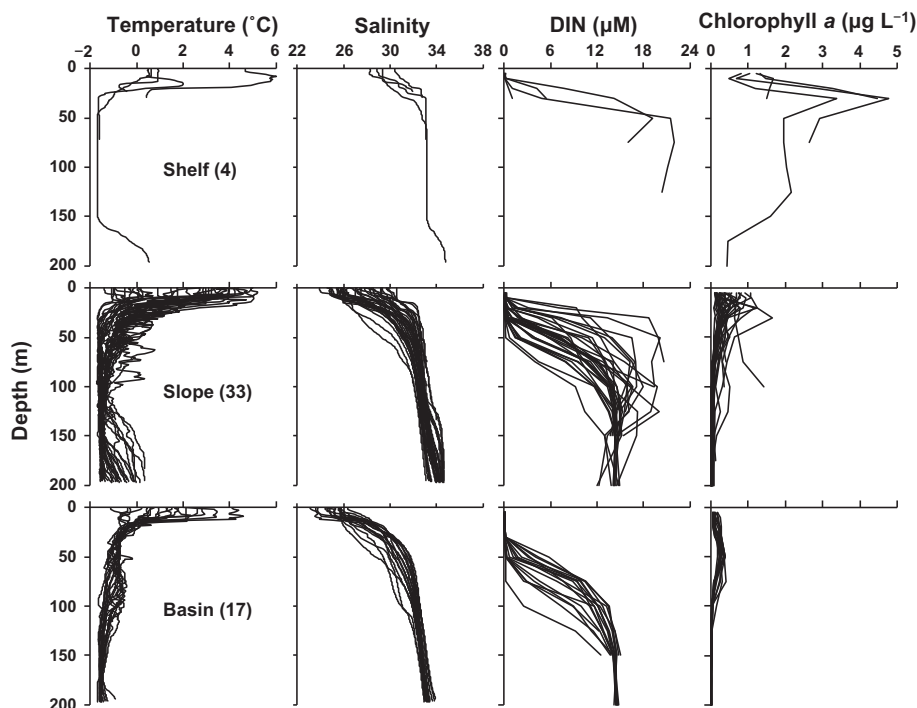


Fig. 8. Vertical profiles of temperature, salinity, dissolved inorganic nitrogen (DIN) and chlorophyll *a* at each station in each of the three regions in the western Arctic Ocean during August–October 2008: Shelf (upper), Slope (middle) and Basin (lower). The three regions were identified from the cluster analysis of copepod abundance using a Bray–Curtis similarity (see Fig. 5). The number of included stations for each region are shown in parentheses.

and Chl. *a*. Sea surface salinity was low in the order of Basin < Slope < Shelf. DIN at the surface was low in all regions, but vertical profiles varied between regions. DIN increased to 12 μM deeper than 50 m in the Shelf and Slope regions, while DIN depletion was more severe in the Basin region. Chl. *a* values were related to the nutrient profiles, with a Chl. *a* peak ($>1 \mu\text{g L}^{-1}$) observed in the upper 50 m both in the Shelf and Slope regions, with a low peak (about $0.5 \mu\text{g L}^{-1}$) at the subsurface layer (ca. 60 m) in the Basin region.

Because the DIN at the surface was depleted in all regions, the present study period (26 August to 8 October) is considered to be the post spring-summer bloom. However, regional differences in DIN concentration (Shelf > Slope > Basin) suggest that the high nutrient concentrations found in the subsurface layer originated from Pacific Water (Coachman and Barnes, 1961; Kinney et al., 1970). Thus the nutrient concentration, phytoplankton stock and also zooplankton community in the summer western Arctic Ocean seem to be strongly controlled by the distribution of water masses.

A schematic diagram of the horizontal distributions of water mass, phytoplankton, and copepod population structure in the western Arctic Ocean during the summer is shown in Fig. 9. Since Pacific Water contains high nutrients, phytoplankton has a relatively high peak near the surface layer in the Shelf and Slope regions (Springer and McRoy, 1993). Under these food conditions, Arctic large-sized copepods *C. glacialis* and *M. longa* have active reproduction, resulting in high abundance and dominance of early copepodid stages. The small-sized copepod *Pseudocalanus* spp. is also thought to have active reproduction, resulting in

high abundance in the Shelf and Slope. The nutrient concentration in Pacific Water is decreased and depleted towards the north and may not reach the Basin region. As a result of these conditions, the nutrient concentration is low and phytoplankton has a small peak in the subsurface layer of the Basin region. Under such limited food conditions, the magnitude of reproduction of copepods is considered to be small. This implies a low abundance of small-sized copepods (*Pseudocalanus* spp.) and dominance of late copepodid stages of large copepods in the Basin.

In conclusion, this study revealed that the zooplankton community in the summer western Arctic Ocean was largely divided into two regions: the Shelf/Slope and Basin. Regional differences in zooplankton community may be regulated by the amount of phytoplankton, which is in turn related to the nutrient supply from Pacific Water. Nutrients supplied by Pacific Water decreased and were depleted towards the north. Phytoplankton standing stock also showed a similar regional distribution. Under these food conditions, the magnitude of copepod reproduction is thought to be greater in the Shelf and Slope than in the Basin region. Thus, the copepod community showed high abundance with early copepodid stages in the Shelf and Slope regions, with low abundance and late copepodid stages in the Basin region. These results indicate that the zooplankton community structure in the summer western Arctic Ocean is mainly governed by the physical and chemical condition of the water masses. Recent sea ice reduction in the western Arctic Ocean caused drastic changes in nutrient and phytoplankton distribution through Arctic Ocean circulation and eddies (Nishino et al., 2011a, 2011b). Therefore, the reduction of sea ice coverage has potential to change the horizontal distribution of the copepod community. Continuous monitoring is needed to evaluate this possible effect in the future.

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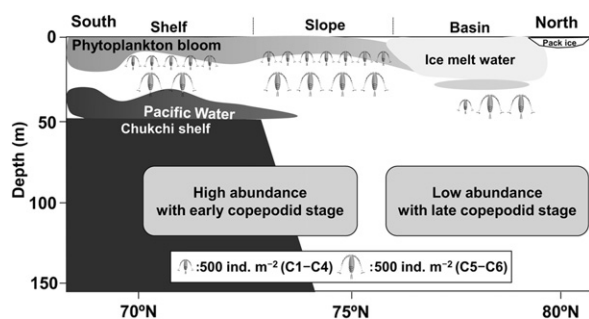


Fig. 9. Schematic diagram showing regional variation in abundance and population structure of Arctic copepods (*C. glacialis*) in the western Arctic Ocean during August–October 2008. Numbers of small- and large-sized symbols represent the amount of abundance (500 ind. m^{-2} per symbol) of early (C1–C4) and late (C5–C6) copepodid stages, respectively.

References

- Ashjian, C.J., Campbell, R.G., Welch, H.E., Butler, M., Keuren, D.V., 2003. Annual cycle in abundance, distribution, and size in relation to hydrography of important copepod species in the western Arctic Ocean. *Deep-Sea Res. I* 50, 1235–1261.
- Auel, H., Hagen, W., 2002. Mesozooplankton community structure, abundance and biomass in the central Arctic Ocean. *Mar. Biol.* 140, 1013–1021.
- Båmstedt, U., Ervik, A., 1984. Local variations in size and activity among *Calanus finmarchicus* and *Metridia longa* (Copepoda, Calanoida) overwintering on the west coast of Norway. *J. Plankton Res.* 6, 843–857.
- Barthel, K.-G., 1988. Feeding of three *Calanus* species on different phytoplankton assemblages in the Greenland Sea. *Meeresforschung/Rep. Mar. Res.* 32, 92–106.
- Bray, J.B., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27, 325–349.
- Brodsky, K.A., 1967. Calanoida of the Far-eastern Seas and Polar Basin of the USSR. Israel Program Scientific Translation, Jerusalem.
- Campbell, R.G., Sherr, E.B., Ashjian, C.J., Plourde, S., Sherr, B.F., Hill, V., Stockwell, D.A., 2009. Mesozooplankton prey preference and grazing impact in the western Arctic Ocean. *Deep-Sea Res. II* 56, 1274–1289.
- Coachman, L.K., Barnes, C.A., 1961. The contribution of Bering Sea water to the Arctic Ocean. *Arctic* 14, 147–161.
- Comiso, J.C., Parkinson, C.L., Gersten, R., Stock, L., 2008. Accelerated decline in the Arctic sea ice cover. *Geophys. Res. Lett.* 35, L01703. doi:10.1029/2007GL031972.
- Conover, R.J., Huntley, M., 1991. Copepods in ice-covered seas – distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. *J. Mar. Syst.* 2, 1–41.
- Cota, G.F., Pomeroy, L.R., Harrison, W.G., Jones, E.P., Peters, F., Sheldon Jr., W.M., Weingartner, T.R., 1996. Nutrients, primary production and microbial heterotrophy in the southeastern Chukchi Sea: Arctic summer nutrient depletion and heterotrophy. *Mar. Ecol. Prog. Ser.* 135, 247–258.
- Dawson, J.K., 1978. Vertical distribution of *Calanus hyperboreus* in the central Arctic ocean. *Limnol. Oceanogr.* 23, 950–957.
- Falk-Petersen, S., Pedersen, G., Kwasniewski, S., Hegseth, E.N., Hop, H., 1999. Spatial distribution and life cycle timing of zooplankton in the marginal ice zone of the Barents Sea during the summer melt season in 1995. *J. Plankton Res.* 21, 1249–1264.
- Falk-Petersen, S., Mayzaud, P., Kattner, G., Sargent, J.R., 2009. Lipids and life strategy of Arctic *Calanus*. *Mar. Biol. Res.* 5, 18–39.
- Field, J.G., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analyzing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.* 8, 37–52.
- Frost, B.W., 1989. A taxonomy of the marine calanoid copepod genus *Pseudocalanus*. *Can. J. Zool.* 67, 525–551.
- Grainger, E.H., 1959. The annual oceanographic cycle at Igloolik in the Canadian Arctic. I. The zooplankton and physical and chemical observations. *J. Fish. Res. Board Can.* 16, 453–501.
- Grønvik, S., Hopkins, C.C.E., 1984. Ecological investigations of the zooplankton community of Balsfjorden, northern Norway: generation cycle, seasonal vertical distribution, and seasonal variations in body weight and carbon and nitrogen content of the copepod *Metridia longa* (Lubbock). *J. Exp. Mar. Biol. Ecol.* 80, 93–107.
- Haq, S.M., 1967. Nutritional physiology of *Metridia lucens* and *M. longa* from the Gulf of Maine. *Limnol. Oceanogr.* 12, 40–51.
- Hill, V., Cota, G., 2005. Spatial patterns of primary production on the shelf, slope and basin of the western Arctic in 2002. *Deep-Sea Res. II* 52, 3344–3354.
- Hirche, H.-J., Niehoff, B., 1996. Reproduction of the Arctic copepods *Calanus hyperboreus* in the Greenland sea-field and laboratory observations. *Polar Biol.* 16, 209–219.
- Hopcroft, R.R., Kosobokova, K.N., Pinchuk, A.I., 2010. Zooplankton community patterns in the Chukchi Sea during summer 2004. *Deep-Sea Res. II* 57, 27–39.
- Hunt Jr., G.L., Drinkwater, K., 2007. Introduction to the proceedings of the GLOBEC symposium on effects of climate variability on sub-Arctic marine ecosystems. *Deep-Sea Res. II* 54, 2453–2455.
- Kinney, P., Arhelger, M.E., Burrell, D.C., 1970. Chemical characteristics of water masses in the Amerasian Basin of the Arctic Ocean. *J. Mar. Res.* 75, 4097–4104.
- Kosobokova, K., Hirche, H.-J., 2000. Zooplankton distribution across the Lomonosov Ridge, Arctic Ocean: species inventory, biomass and vertical structure. *Deep-Sea Res. I* 47, 2029–2060.
- Lane, P.V.Z., Llinás, L., Smith, S.L., Pilz, D., 2008. Zooplankton distribution in the western Arctic during summer 2002: hydrographic habitats and implications for food chain dynamics. *J. Mar. Syst.* 70, 97–133.
- Longhurst, A., Sameoto, D., Herman, A., 1984. Vertical distribution of Arctic zooplankton in summer: eastern Canadian archipelago. *J. Plankton Res.* 6, 137–168.
- Lowry, L.F., Sheffield, G., George, C., 2004. Bowhead whale feeding in the Alaskan Beaufort Sea, based on stomach contents analyses. *J. Cetacean Res. Manage.* 6, 215–223.
- Marin, V., 1987. The oceanographic structure of eastern Scotia Sea-IV. Distribution of copepod species in relation to hydrography in 1981. *Deep-Sea Res. A* 34, 105–121.
- Markus, T., Stroeve, J.C., Miller, J., 2009. Recent changes in Arctic sea ice melt onset, freezeup, and melt season length. *J. Geophys. Res.* 114, C12024. doi:10.1029/2009JC005436.
- Matsuno, K., Yamaguchi, A., Hirawake, T., Imai, I., 2011. Year-to-year changes of the mesozooplankton community in the Chukchi Sea during summers of 1991, 1992 and 2007, 2008. *Polar Biol.* 34, 1349–1360.
- McLaren, I.A., Laberge, E., Corkett, C.J., Seigney, J.M., 1989. Life cycle of four species of *Pseudocalanus* in Nova Scotia. *Can. J. Zool.* 67, 552–558.
- Motoda, S., 1959. Devices of simple plankton apparatus. *Mem. Fac. Fish. Hokkaido Univ.* 7, 73–94.
- Nishino, S., Itoh, M., Kawaguchi, Y., Kikuchi, T., Aoyama, M., 2011a. Impact of an unusually large warm-core eddy on distributions of nutrients and phytoplankton in the southwestern Canada Basin during late summer/early fall 2010. *Geophys. Res. Lett.* 38, L16602. doi:10.1029/2011GL047885.
- Nishino, S., Kikuchi, T., Yamamoto-Kawai, M., Kawaguchi, Y., Hirawake, T., Itoh, M., 2011b. Enhancement/reduction of biological pump depends on ocean circulation in the sea-ice reduction regions of the Arctic Ocean. *J. Oceanogr.* 67, 305–314.
- Norrbin, M.F., 1994. Seasonal patterns in gonad maturation, sex ratio and size in some small, high latitude copepods: implications for overwintering tactics. *J. Plankton Res.* 16, 115–131.
- Norrbin, M.F., 1996. Timing of diapauses in relation to the onset of winter in the high-latitude copepods *Pseudocalanus acuspes* and *Acartia longiremis*. *Mar. Ecol. Prog. Ser.* 142, 99–109.

- Norrbin, M.F., Olsen, R.E., Tande, K.S., 1990. Seasonal variation in lipid class and fatty acid composition of two small copepods in Balsfjorden, northern Norway. *Mar. Biol.* 105, 205–211.
- Omori, M., 1969. Weight and chemical composition of some important oceanic zooplankton in the North Pacific Ocean. *Mar. Biol.* 3, 4–10.
- Renz, J., Hirche, H.-J., 2006. Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I. Seasonal and spatial distribution. *Mar. Biol.* 148, 567–580.
- Renz, J., Peters, J., Hirche, H.-J., 2007. Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: II. Reproduction, growth and secondary production. *Mar. Biol.* 151, 515–527.
- Richter, C., 1994. Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. *Ber. Polarforsch.* 154, 1–87.
- Richter, C., 1995. Seasonal changes in the vertical distribution of mesozooplankton in the Greenland Sea Gyre (75°N): distribution strategies of calanoid copepods. *ICES J. Mar. Sci.* 52, 533–539.
- Sell, A.F., Van Keuren, D., Madin, L.P., 2001. Predation by omnivorous copepods on early developmental stages of *Calanus finmarchicus* and *Pseudocalanus* spp. *Limnol. Oceanogr.* 46, 953–960.
- Shannon, C.E., Weaver, W., 1949. *The Mathematical Theory of Communication*. The University of Illinois Press, Urbana.
- Shimada, K., Carmack, E.C., Hatakeyama, K., Takizawa, T., 2001. Varieties of shallow temperature maximum waters in the western Canadian Basin of the Arctic. *Geophys. Res. Lett.* 28, 3441–3444.
- Shimada, K., Kamoshida, T., Itoh, M., Nishino, S., Carmack, E., McLaughlin, F., Zimmermann, S., Proshutinsky, A., 2006. Pacific Ocean inflow: influence on catastrophic reduction of sea ice cover in the Arctic Ocean. *Geophys. Res. Lett.* 33, L08605. doi:10.1029/2005GL0256254.
- Springer, A.M., McRoy, C.P., 1993. The paradox of pelagic food webs in the northern Bering Sea-III. Patterns of primary production. *Cont. Shelf Res.* 13, 575–599.
- Springer, A.M., McRoy, C.P., Turco, K.R., 1989. The paradox of pelagic food web in the northern Bering Sea-II. Zooplankton communities. *Cont. Shelf Res.* 9, 359–386.
- Stroeve, J., Holland, M.M., Meier, W., Scambos, T., Serreze, M., 2007. Arctic sea ice decline: faster than forecast. *Geophys. Res. Lett.* 34, L09501. doi:10.1029/2007GL029703.
- Vinogradov, M.E., 1997. Some problems of vertical distribution of meso- macroplankton in the ocean. *Adv. Mar. Biol.* 32, 1–92.
- Wassmann, P., Reigstad, M., Haug, T., Rudels, B., Carroll, M.L., Hop, H., Gabrielsen, G.W., Falk-Petersen, S., Denisenko, S.G., Arashkevich, E., Slagstad, D., Pavlova, O., 2006. Food webs and carbon flux in the Barents Sea. *Prog. Oceanogr.* 71, 232–287.
- Woodgate, R.A., Weingartner, T., Lindsay, R., 2010. The 2007 Bering Strait oceanic heat flux and anomalous Arctic sea-ice retreat. *Geophys. Res. Lett.* 37, L01602. doi:10.1029/2009GL041621.
- Yamaguchi, A., Ikeda, T., Shiga, N., 1998. Population structure and life cycle of *Pseudocalanus minutus* and *Pseudocalanus newmani* (Copepoda: Calanoida) in Toyama Bay, southern Japan Sea. *Plankton Biol. Ecol.* 45, 183–193.
- Yamaguchi, A., Shiga, N., 1997. Vertical distributions and life cycles of *Pseudocalanus minutus* and *P. newmani* (Copepoda; Calanoida) off Cape Esan, southwestern Hokkaido. *Bull. Plankton Soc. Jpn.* 44, 11–20 (in Japanese with English abstract).

